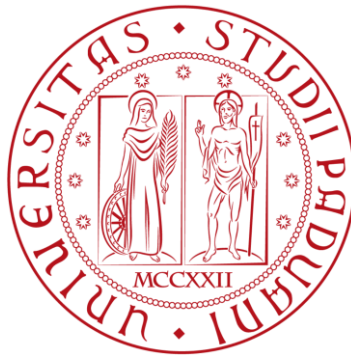


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**TESI DI LAUREA**

**Influence of Pack Size on the Behavior of *Canis lupus* in Response to  
Anthropogenic Stimuli in a Natural Environment**

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*Wolfs eyes are mirrors; what different people see in them is simply a reflection of ourselves. Could they reflect even more, not just a person's attitudes towards wolves, but towards the environment, wild lands, nature itself?" (Theberge 1998:10).*

# Summary

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## Riassunto

La paura negli animali gioca un ruolo cruciale nella struttura delle comunità ecologiche, influenzando dinamiche complesse negli ecosistemi. I lupi, tra i carnivori sociali più studiati al mondo, offrono un caso emblematico: le loro risposte comportamentali possono generare effetti a cascata sugli ecosistemi. Sebbene conosciamo molto sul modo in cui i lupi si muovono e si adattano a paesaggi alterati dall'uomo, le influenze umane sulle loro dinamiche sociali rimangono ancora in gran parte inesplorate.

Questo studio si concentra sulla paura indotta dall'uomo nei lupi italiani (*Canis lupus italicus*), analizzando come la presenza del branco moduli le loro risposte a stimoli sonori che segnalano l'immediata presenza umana. Attraverso esperimenti acustici controllati, l'indagine esplora le risposte comportamentali sia individuali che collettive alla paura, ipotizzando che i lupi in branco mostrino una minore probabilità di mostrare risposte di paura e spendano meno tempo nella valutazione del rischio rispetto a quelli isolati. Questi risultati contribuiranno a una comprensione più approfondita delle interazioni tra comportamento animale e impatti antropogenici, con implicazioni per la conservazione e la gestione degli ecosistemi naturali e dei conflitti uomo-animale selvatico.

## Abstract

Fear in animals plays a crucial role in the structure of ecological communities, influencing complex dynamics within ecosystems. Wolves, among the most studied social carnivores in the world, provide an emblematic case: their behavioral responses can generate cascading effects on ecosystems. While we know much about how wolves move and adapt to human-altered landscapes, the human influences on their social dynamics remain largely unexplored. This study focuses on human-induced fear in Italian wolves (*Canis lupus italicus*), examining how pack size shapes their ability to cope with these stimuli. Through controlled acoustic experiments, the research explores both individual and collective behavioral responses to fear, hypothesizing that wolves in packs are more resilient than those that are isolated. These findings will contribute to a deeper understanding of the interactions between animal behavior and anthropogenic impacts, with implications for the conservation and management of natural ecosystems and human-wildlife conflicts.

## INTRODUCTION

### The Italian Wolf

The grey wolf (*Canis lupus* L., 1758) is a placental mammal belonging to the order of carnivores. Its behavioral flexibility and opportunistic, generalist nature have led to a historical distribution that once spanned almost the entire Northern Hemisphere (MacNulty et al., 2020; Paquet & Carbyn, 2003). Nuclear and mitochondrial DNA studies have shown that the Apennine population, in central Italy, is distinct from other Eurasian populations, leading it to be classified as a subspecies: *Canis lupus italicus* (Randi & Lucchini, 2012; Fabbri et al., 2007; Montana et al., 2017).

Its historical distribution in southern Europe, comprised the Italian peninsula particularly in the northern (Alpine) and central (Apennine) mountain ranges. Wolves were progressively eradicated throughout Western Europe and the Alps during the 18th and 19th centuries (Boitani, 2003). Italy's first wildlife legislation concerning hunting and wildlife, dating back to 1923, classified the wolf, along with other predators, as a "harmful species", thus permitting its killing by any means. Surviving populations persisted in two isolated areas in the Southern Apennines, reaching its minimum population size of less than 100 individuals reported in the 1970s (Boitani 1984; Boitani 1992; Zimen and Boitani 1975). In 1971 it was removed from the list of harmful species, prohibiting hunting and the use of poisoned bait, and in 1979, the Bern Convention included the wolf in Appendix II : 'strictly protected species', officially recognizing its ecological value (Allen, 1979; Mech, 1970; Rutter & Pimlott, 1968). From a conservation perspective, it has been studied how restored wolf populations bring significant ecological benefits. Wolves contribute to the ecosystem by exerting selective pressure, leading to cascading effects (Gaynor et al., 2019; Fortin et al., 2005). For example, wolves contribute to ecosystem dynamics by creating scavenging opportunities for other species through wolf-killed carcasses and triggering trophic cascades (Ripple et al., 2001). The wolf-driven ungulates culling leads to the regeneration of woody riparian vegetation, which provides nesting habitats for songbirds and supports broader ecological functions. By regulating prey populations and fostering diverse plant communities, wolves enhance biodiversity and promote the development of more complex, resilient ecosystems (Wilmers et al., 2005; Ripple et al., 2004).

In 2008, wolves were classified as a "vulnerable" species on the International Union for Conservation of Nature (IUCN) Red List. Following the protection laws, the wolf population in Italy has shown remarkable recovery. Nowadays, wolves are continuously distributed along the major mountain ranges of Italy (Fabbri et al., 2007; Marucco et al., 2022, Boitani, 2022). Today, ISPRA (Italian Institute for Environmental Protection and Research) estimates that

there are over 3,000 wolves in Italy, with the most notable increase recorded in the Alps. Approximately 950 of these wolves are located in alpine regions, while nearly 2,400 are distributed throughout the rest of the peninsula (La Morgia et al., 2022). Nevertheless, recent studies employing more comprehensive estimation models challenge the figures reported by ISPRA, suggesting that the Alpine and Italian wolf population is approximately 4,232 (Mergeay et al., 2024).

Despite this recovery, the conflict with human economies has historically been the main reason behind wolf control measures (Boitani, 2000), and human-related activities remain the leading cause of wolf mortality in Italy (Musto et al. 2021). Currently, it is listed as Least Concern (IUCN, 2023) and Council of Europe's Bern Convention Committee has adopted an EU proposal to modify the status of wolf protection from "strictly protected fauna species" (Appendix II) to "protected fauna species" (Appendix III) (European Union, 2024; Secretariat of the Bern Convention, 2024).

### **The Social Unit: An Overview**

Characterized by tight social bonds, the life of a wolf revolves around the pack, their primary social structure. This structure is formed generally by a multigenerational family (Stahler, Smith, et al., 2020). The number of individuals, the age structure, composition, and degree of cohesion in the pack can range widely, as do the foraging strategies, such as prey selection, hunting methods, and scavenging behaviors. This variation is highly context-dependent, influenced by factors such as ecological systems, seasons, prey characteristics (type, size, and density), the density of conspecifics and competitors, landscape features, and the degree of anthropogenic disturbance (Borg et al., 2015; Stahler, Smith, et al., 2020; Thurber et al., 1994). The theory suggests that animals form groups when the benefits of living together outweigh the costs of intra-group competition (Markham et al., 2015). By living in groups and displaying cooperative social behaviors, individuals can increase their fitness, which is their ability to survive and reproduce in a given environment. This fitness advantage is particularly evident in wolves, where group living provides numerous benefits across various environments, including aiding in territorial defense, cooperative breeding, hunting, and food protection (Cassidy et al., 2015; Mech & Boitani, 2003, Clutton-Brock, 2002; Mech, 1970; MacNulty et al., 2012, 2014; Vucetich et al., 2004).

At its core, a wolf pack consists of a breeding pair and their offspring, which usually includes a balanced proportion of males and females. The dominant pair of wolves, often referred to as the alpha male and female, are the leaders of the pack. Their dominance is established through social interactions, physical displays, and hierarchical behavior. This pair is male and female because they are the ones that mate and breed during the winter, giving birth to pups in the spring. Offspring of varying ages may stay with the pack for several years, gradually

forming a multigenerational family unit. This family structure typically includes first-order relatives, such as siblings and parents with their offspring, as well as second-order relatives, including half-siblings and grandparent-grandoffspring pairs (Stahler, Smith, et al., 2020). Pack composition and size are not fixed; they fluctuate within and across ecosystems in response to natural factors (Tallian. et al., 2023). This is critical because alterations to pack size and structure can directly affect a pack's ability to hunt efficiently, rear offspring, and defend its territory. Moreover, these changes can ripple through their overall ecology, influence population dynamics, and create cascading effects across entire ecosystems (Hayes et al., 1991).

### **Fear Dynamics and Social Buffering**

Fear is an emotional state often triggered by the perception of danger and manifests through a variety of behaviors aimed at promoting survival. Although we cannot directly assess an emotional state of an animal, behavioral responses like fleeing, freezing, startling or hiding have energetical and ecological costs (Stankowich & Blumstein, 2005; Blumstein 2020) like signalling one's presence to potential prey and predators or disrupting foraging behaviors, potentially yielding resources to competitors (Blumstein, 2020; Bovo, 2024). Thus, these behaviors should be performed only if motivated by the intent of avoiding a perceived risk, potentially outweighing the costs associated with them (Cooper and Frederick, 2007; Blumstein, 2020; Lima and Dill 1990; Ydenberg and Dill, 1986). For these reasons, we can consider this type of behaviors as fearful responses. Given the costs of performing fearful responses, animals must carefully assess the risks of a situation before reacting with fear (Stankowich & Blumstein, 2005). One such strategy involves behaviors like pausing, observing, sniffing, or maintaining a wary posture evaluating a potential threat (Stankowich & Blumstein, 2005). *Risk assessment* refers to all actions performed with the goal of evaluating and understanding the potential implications of a situation or object (Blumstein, 2020; Chan et al., 2010). It is crucial from an ecological and evolutionary perspective, as it allows animals to evaluate the likelihood of danger while exploiting resources or navigating novel environments (Stankowich & Blumstein, 2005).

When faced with danger or stress, the presence of conspecifics can act as a powerful buffer, signaling safety and support ( Kikusui et al., 2006). Studies have shown that the presence or cues from an affiliative group members can alleviate stress responses in various social species (Young et al., 2014; Martin et al., 2023; Kikusui et al., 2006; Gilmour et al., 2022), a phenomenon known as “social buffering” (Hennessy et al., 2009). According to Hennessy et al. (2009), multiple factors influence social buffering, these include the species social

organization, past experiences, sex, the degree of integration into a social group, and the developmental stage at which individual responses are assessed. Jean-Joseph (2020) evidence how wolves experience heightened arousal when alone, reflected in increased heart rate (HR) and decreased heart rate variability (HRV), compared to when accompanied by conspecifics, highlighting the mitigating effect of social presence on stress responses (Jean-Joseph H., 2020). Further scientific research on captive wolves and wild wolves suggest that both exhibit lower levels of neophobia, the fear of new stimuli, when in the company of conspecifics with individual factors such as rank and age influencing this response (Moretti et al., 2015; Zorzi, 2022). So, investigation has demonstrated how there is a positive correlation between affiliative relationships and stress buffering, as well as social support seeking (Forss et al., 2017; Moretti et al., 2015; Sergeyev et al., 2020).

In predator-prey systems, prey show anti-predator behaviors such as vigilance and fear behaviors, to minimize the risk of predation (Ydenberg and Dill, 1986; Cooper and Frederick, 2007; Laundre et al., 2010). Anti-predator behaviors are not exclusive to prey species; even apex predators exhibit such behaviors to mitigate risks from intra-guild aggression (Frid and Dill, 2002; Mech and Boitani, 2003) and human-induced disturbances (Gill et al., 1996; Frid and Dill, 2002). Even for wolves, encountering humans still pose significant risks; lethal control, poaching, and traffic collisions are the primary causes of wolf mortality (Blanco & Sundseth, 2023). Consequently, human disturbances are expected to elicit anti-predator responses in wolves due to the potentially lethal nature of these threats (Frid and Dill, 2002).

### **Human-Wildlife Conflict Context**

Human activities have profoundly altered wildlife behavior and ecology, disrupting the global distribution and activity patterns of many animal species (Dirzo et al., 2014; Gaynor et al., 2018; Tucker et al., 2018). The pervasive human footprint on the landscape, including urbanization and land use changes, represent a major threat to wildlife virtually across all taxonomic groups (Hansen et al., 2005; Fischer and Lindenmayer, 2007; T. Newbold et al., 2015; J.E Watson et al., 2016). The effects of urbanization are felt not just through habitat loss and fragmentation but also because urban areas serve as hubs of anthropogenic disturbance, including threats (real or perceived) that provoke antipredator reactions (Frid and Dill, 2002; Greggor et al., 2020). Yet, human impacts extend beyond developed areas, as it has been shown that the mere presence of humans has impacted wildlife behavior and activity even in wildland areas (Suraci et al., 2019; Sih et al., 2010).

Darimont et al. (2015) describe humans as “super-predators” due to their unique hunting strategies, which differ fundamentally from those of non-human predators. Unlike natural



predators that typically target vulnerable individuals (e.g., the sick, old, or weak), humans often employ advanced technology, hunt disproportionately large and reproductive individuals, and do so at rates that exceed the natural replacement of prey populations.. Furthermore, the influence of humans as “super-predators” on prey communities extends beyond direct impacts and can be understood through the lens of the “ecology of fear” framework (Blumstein, 2020; Clinchy et al., 2016; Crawford et al., 2022). This concept highlights how the presence of predators, in this case humans, shapes prey behavior and ecology indirectly, altering patterns of movement, habitat use, foraging time and even population dynamics (Brown et al., 1999; Darimont et al., 2015).

Research has extensively documented the impacts of habitat destruction and defaunation on species and ecosystems (Dirzo et al., 2014). However, the indirect, nonlethal mechanisms by which humans influence the natural world remain largely unquantified. The persecution of wolves across Europe, particularly in Italy, led to their near-extirpation by the 1970s (Boitani, 1984; Zimen & Boitani, 1975), and despite population recovery, human-wildlife conflicts persist. Beyond direct mortality, human presence continues to shape wolf behavior through fear-driven responses, reinforcing their avoidance of humans even in the absence of immediate threats (Versluijs et al., 2022). In regions where wildlife and humans overlap, animals may minimize risk not by relocating but by adjusting their behavior temporally, such as altering their activity patterns to avoid human presence (Kronfeld-Schor et al., 2003; Lambert et al., 2021), leading to spatiotemporal separation between wolves and humans (Lesmerises et al., 2012; Milleret et al., 2019; Carricondo-Sanchez et al., 2020). For instance, recent research demonstrates that human-induced fear causes a shift towards nocturnal behavior in many wild mammal species, especially for large carnivores (Gaynor et al., 2018; Nickel et al., 2020; Suraci et al., 2019), or that exposure to human voices can significantly reduce feeding time in large carnivores, leading to incomplete carcass consumption (Smith et al., 2017). This disruption forces the predator to increase their kill rates, which can alter predator-prey dynamics and affect the ecological balance of the wildlife community (Smith et al., 2015; Smith et al., 2017).

The impact of anthropogenic stress on wolves’ social dynamics is particularly significant, as few wolf populations persist in landscapes untouched by human influence (Tallian et al., 2023). While wolves are often regarded as a resilient species, capable of rebounding quickly after population reductions (Fuller, 1989; Fuller et al., 2003), their apparent numerical resilience masks the fragility of their social structure and pack composition. This is critical because alterations to pack size and stability can disrupt the mechanisms by which wolves collectively assess and respond to risks, potentially increasing their vulnerability to fear-induced

disruptions (Hayes, 1991). Moreover, changes in pack composition can propagate through their overall ecology, influence population dynamics, and create cascading effects across entire ecosystems (Hebblewhite et al., 2005; Fernández-Gil et al., 2016, 2020; Milleret et al., 2017, Ordiz et al., 2013, 2021). Human activities may disrupt social structures, leading to group instability and contributing to population declines (Snijders et al. 2017). Disruptions to pack integrity may exacerbate fear responses, further destabilizing the group and undermining its ecological functions. Thus, understanding the roles that pack dynamics play in shaping risk assessment and fearful responses is vital. If packs mitigate the disruptive effects of fear, preserving their social integrity becomes essential not only for the stability of wolf populations but also for maintaining their ecological role in human-impacted environments.

### **Aims of the study**

This study investigates how the pack influences how wolves perceive a threat like the immediate human presence, offering a novel perspective on how the presence of the pack influences individual vulnerability to human-induced fear (Moretti et al., 2015; Gaynor et al., 2018). Increasing knowledge about behavioral responses of wolves toward humans might improve appropriate management and decrease conflicts related to fear of wolves and contribute to finding an ecological balance in shared landscapes (Musiani et al., 2009; Treves and Bruskotter, 2011).

In our study, we exposed wild wolves to an acoustic test utilizing a modern device, called *boombox*, consisting of a speaker connected to camera traps, to examine their behavioral responses to playback human voice. The experimental trials were alternated with control conditions featuring bird sounds and periods of baseline without sounds. Consistent with previous research on carnivores and predators, we anticipated that wolves would exhibit pronounced fear responses to human disturbance compared to the control condition involving bird sounds (Crawford et al., 2022; Versluijs et al., 2022). Behavioral observations were categorized into two distinct models: "Fear" and "Vigilant" (Table 1). For reasons discussed above, the "Fear" category captures behaviors indicative of a marked distress in response to a potentially alarming stimulus, (e.g startle, change direction or run). In contrast, the "Vigilant" category indicates a state in which are performed actions aimed at evaluating the potential threat posed by the stimulus, such as pausing, orienting towards the sound, or engaging in cautious observation (Brown et al., 1999; Stankowich & Blumstein, 2005). Observations involving a single individual were labeled as "solitary," while those involving two or more individuals were designated as "group." To quantitatively assess these behavioral responses, we fitted two Generalized Linear Mixed Models (GLMMs). The first model examined the *proportion of time spent vigilant*, while the second analyzed the *probability of a fearful behavior occurrence*. As control variables, we included time of day (night/day) to account for potential

differences in risk perception between nocturnal and diurnal periods (Gaynor et al., 2018), sound event number, which represented how many times the speaker had played a sound since the beginning of the test condition to control for potential habituation effects, and the degree of urbanization of the site, to account for potential variation in animals' responses based on their exposure to human-altered environments.

## MATERIALS AND METHODS

### Study area and test sites

Data collection took place in Tuscany, Central Italy housing a population of 3.647 million human residents. The study area covers approximately 23,000 km<sup>2</sup> and is characterized by medium to high human population density, averaging around 160 individuals per km<sup>2</sup> (IRPET., 2023). The region is bordered to the north and east by the Apennine Mountain range. Tuscany's landscape is predominantly hilly, covering approximately 66.5% of the territory. It also contains significant plains, about 8.4%, and prominent mountain ranges, which make up 25.1% of the region. Data was collected during the period from April to August over two consecutive years. In 2022, 10 sites were selected, while 14 sites were chosen in 2023. However, camera trap thefts led to a reduction in active sites to 9 in 2022 and 13 in 2023. The total of 22 test sites were located across the provinces of Pistoia, Prato, Florence, and Pisa, each exhibiting varying levels of urbanization and human activity (Figure 1). Historically in this scenario, wolves were restricted to mountainous and hilly regions, but they have since broadened their range to cover almost the entire area, including several urbanized zones (Zanni et al., 2023).

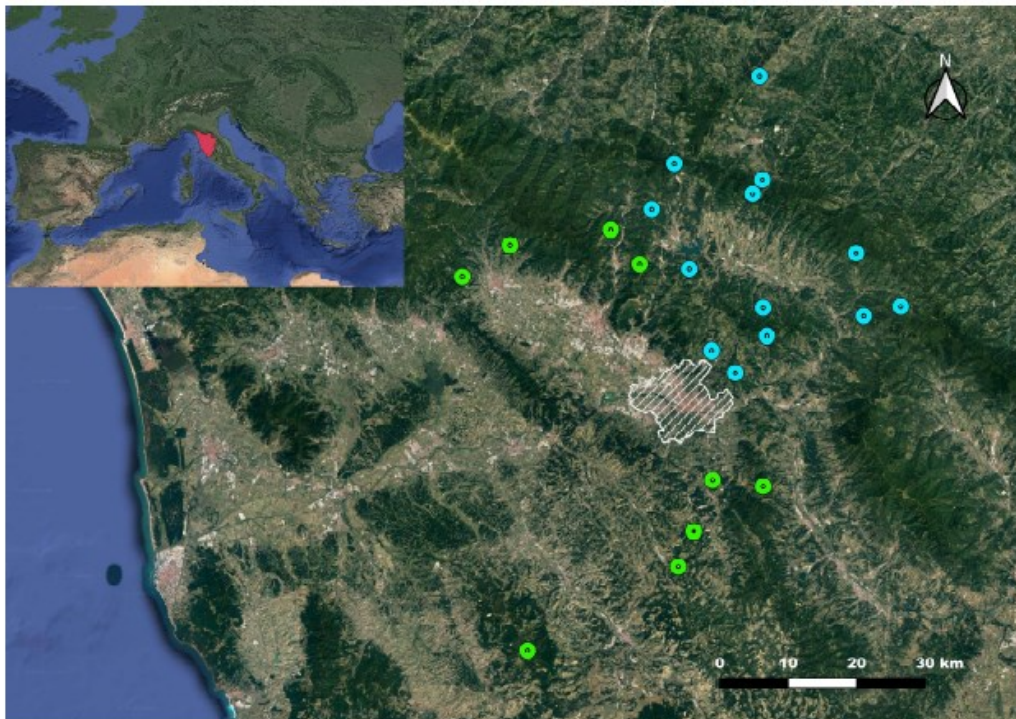


Figure 1. Distribution of test sites over the two-year period (green dots: 2022, light blue dots: 2023), with Florence (shown in white) representing the largest metropolitan area in Tuscany.

Test sites were selected along wooded trails and intersections frequently used by both humans and wildlife, optimizing the likelihood of interactions between the study species and the experimental apparatus. Indicators of wolf activity, including scat, footprints, and scratch marks, were used to confirm the presence of the target species at these sites. Additionally, locations were selected based on their suitability for the strategic placement of two camera traps positioned opposite each other, enabling simultaneous recording from multiple angles. (Pease et al., 2016). To reduce the probability of the sound test overlapping with different sites, locations were selected with a minimum separation distance of 2.5 km (average = 8.6 km). The identification of distinct packs through video footage, using criteria such as pack size, composition, and phenotypic traits, ensured that the same individuals were excluded from being tested at multiple sites.

### **Sampling design**

To record wolves' behavioral responses to sound, two camera traps (Browning Spec Ops Advantage BTC-8A), facing opposite directions, were installed at each designated testing site to increase detection rate, reduce the risk of data loss due to camera malfunctions and to film the scene from different angles (Jacobs & Ausband, 2018; Pease et al., 2016). The cameras were secured to trees using flexible steel cable locks (Master Lock Python 8417Dpro), placed between 1 and 3 meters above ground, oriented to face it from opposite angles spaced between 10 and 20 meters apart, depending on the site characteristics. The camera traps operated continuously over a 24-hour cycle, recording 1-minute clips triggered by the Passive Infrared Sensor (PIR) with no delay between activations. If excessive triggering occurred due to environmental factors like changing light or shadows, the affected camera was adjusted to a shortened and night-shifted operating schedule that primarily accounted for the species predominantly nocturnal behavior. Additionally, the camera traps were equipped with 64 or 128 GB SD cards (with each site always having at least one 128 GB card) and powered by external 12V, 5Ah batteries, both of which were replaced every two weeks. At each site, one of the two camera traps was integrated with a 'boombox' system (Boomboxes by Freaklabs and Meredith Palmer ©) programmed via Arduino software. This setup was directly linked to the PIR motion sensor of the camera trap, activating external speakers to play audio files whenever the sensor detected motion (Palmer et al., 2022).

The testing procedure involved two distinct conditions: control and test. In the control condition, audio playback featured the calls of native birds from the study area, specifically the nightingale (*Luscinia megarhynchos* C. L. Brehm, 1831) and the tawny owl (*Strix aluco* Linnaeus, 1758). The test condition involved the playback of human voices. Both control and test sounds consisted in a randomized playback of 12 different tracks per condition, in the

control condition 6 tracks were of tawny owl and 6 for nightingale. All bird and human voice tracks lasted 5 seconds and were played at a standardized volume of 80 decibels, measured at a distance of 5 cm from the speakers. Each group of tracks was loaded onto the boombox attached to the camera trap, programmed to randomly play one track from the group starting two seconds after the PIR sensor was triggered. This configuration ensured that the camera trap began recording video before the sound played, preventing any loss of animal behavioral reactions.

Sound groups for both control and test conditions were alternated at each site, with two-week baseline periods between each during which no sounds were played. For example, a potential sequence of conditions at a given site could include: control sounds (two weeks), baseline (two weeks), test sounds (two weeks), baseline (two weeks), control sounds (two weeks), baseline (two weeks), and test sounds (two weeks). If issues or malfunctions occurred, the program continued as planned without altering the condition sequence, resulting in data gaps for some conditions at specific sites.

To minimize habituation to the speaker's location, the speaker position was adjusted between conditions. From the first to the second condition, the speaker was moved to a different spot on the same tree (e.g., another branch). Between the second and third conditions, the entire boombox-speaker system was relocated to the second camera, positioned about 10 meters opposite the first. For the transition from the third to the fourth condition, the speaker's position was adjusted slightly again.

### **Video and behavioral analysis**

For each video, the following data were systematically recorded: the camera name, test site, date and time, test conditions, and the number of individuals observed. Due to inconsistencies in determining the sex, age, and social hierarchy of the wolves, these variables were excluded from the coding process. The videos were analyzed using the software application "Wolf Tracker," developed specifically for this project by Dr. Tiago Roldão. This software was designed to streamline the processes of video playback and metadata annotation. Additionally, it automatically generates a Microsoft Excel file containing the encoded data, facilitating the organization and subsequent analysis of the information. In total, 317 videos featuring wolves were extracted using R and subjected to behavioral analysis.

The behaviors of the individuals were systematically coded using the software Boris (Friard & Gamba, 2016, <https://www.boris.unibo.it>), based on videos recorded by both cameras at each test site. Behavior was tracked from the onset to the conclusion of the acoustic stimulus, with

the behaviors of all individuals in each video being meticulously coded. Ten behaviors were identified and included in the statistical analysis (Table 1). These behaviors were then grouped in two categories: "Vigilant" and "Fear." The "Fear" category includes behaviors indicative of an immediate, rapid, and pronounced reaction to the stimulus that may entail substantial energy expenditure, convey self-presence signals to others, or exhibit a tense state in response to the sounds (Blumstein, 2020; Boissy, 1995; Morrow et al., 2015). This category, thus, comprehends a binomial variable which value is 1 when at least one behavior of the "Fear" category was present in the event.

In contrast, "Vigilant" behavior is associated with risk assessment, characterized by actions aimed at determining whether the sound posed a perceived threat (Brown et al., 1999; Stankowich & Blumstein, 2005). "Vigilant" is a continuous variable that is the proportion of time wolves engaged in vigilant behavior relative to their total time visible on camera ("in sight", Table 1). Events were classified as "solitary" when involving a single individual and as "group" when involving two or more individuals.

**Table 1.** Definition of behaviors used for analyses

Behavior	Description	Category
In sight	The subject is visible	
Stop moving	The subject stops moving for at least 2 seconds.	Vigilant
Head up	The subject lifts its head above its shoulders	Vigilant
Look around	The subject moves its head scanning the surroundings	Vigilant
Startle	The subject jumps back (or jumps in general) suddenly (without preparation of the subject)	Fear
Change direction	The subject deviates from the pathway it had after the sound started	Fear
Insecure posture	In the subject the tail is kept on the vertical line of the legs, lower or even tucked.	Fear
Wince	The subject winces	Fear
Slow walk	The subject walks very slowly with cautious movements, stiff back legs	Fear
Run	The subject runs	Fear

## Statistical analysis

We aimed to determine whether the proportion of time wolves spent displaying vigilant behavior while in sight and the likelihood of exhibiting fear behavior varied across different experimental conditions (baseline, control, and test) and with the presence or absence of the

pack. To address this, we employed two GLMMs (generalized linear mixed models) (Dobson & Barnett, 2018). In the ‘Vigilance’ model, the response variable was the proportion of time wolves engaged in vigilant behavior (as the sum of the time spent in every behavior of the “Vigilance” category) relative to their “in sight” time. For the ‘Fearful’ model, the response variable was the probability for the category “Fear” being equal to 1 (at least one behavior in the category being present in the event, Table 1). For both models, the main predictors were the test condition (baseline, control, or test) and whether wolves were alone (“solitary”) or in a pack (“pack”). Control variables included the time of the day, as a two-level category (“night” or “day”), the sound event number, representing how many times the speaker had played a sound since the beginning of that specific test condition, and the level of urbanization (Table 2). In order to quantify this last variable, we employed the Human Footprint Index (HF), as outlined by Mu et al. (2022), that consists of a 1x1 km squares grid system, within which the degree of urbanization is evaluated based on the nature of anthropogenic alterations and human population density. In every cell of the grid the urbanization score is presented as a continuous scale ranging from 0 (lowest degree of urbanization) to 50 (highest degree of urbanization). For every site, we drawn a circular buffer area corresponding to half of the wolf home range (41.32 km square, half from 82.64 km square, Mattioli et al., 2018) and then the urbanization level has been calculated as the mean HF of all the squares included within the buffer area.

**Table 2:** Models variables description

Name	Category	Values
Condition	Categorical	Baseline; Control sounds; Human sounds
Pack	Categorical	Pack; Solitary
Human Footprint	Continuous	[12.76; 33.79]
Time	Categorical	Day; Night
Number event sound	Continuous	[1; 2307]

To account for site-specific and event-specific variability, the test site and individual sound events were included as random intercept effects in both models. This approach allowed us to distinguish the effects of experimental conditions and landscape characteristics on wolves’ vigilant and fear behaviors, while controlling other relevant factors. The models were fitted using R (version 4.1.1; R Core Team, 2021). The model ‘Vigilance’ was fitted with a beta error distribution and logit link function (Bolker, 2008) using the function `glmmTMB` of the R package

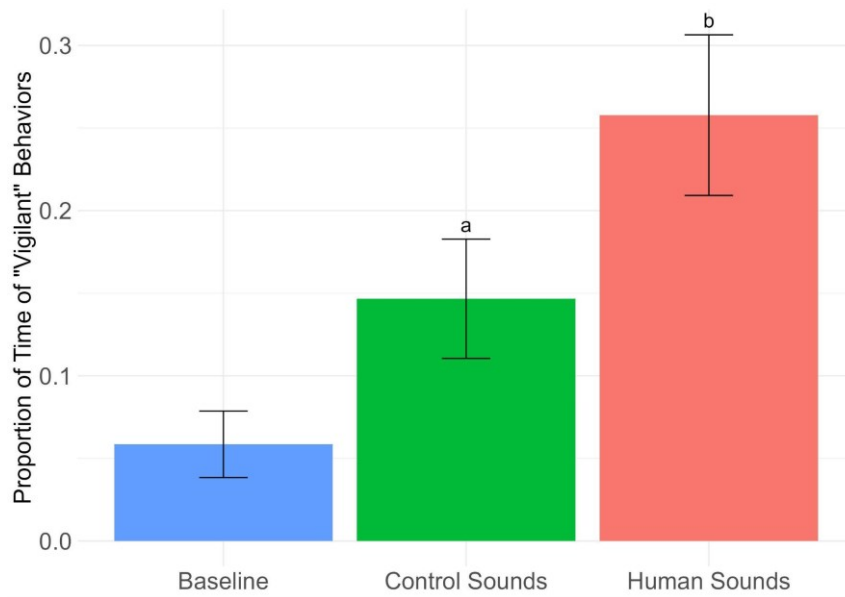


glmmTMB (version 1.0.0; M. Brooks E. et al., 2017). We fitted the model 'Fearflul' using the function `glmer` of the R package `lme4` (Bates et al., 2015).

Since the summary of the models' outputs only the level of significance of the comparison between the baseline and the other conditions, in order to highlight the level of significance of all the comparisons between conditions we used the function *emmeans* from the *emmeans* package in R (version 1.10.7; Russel, L. 2025).

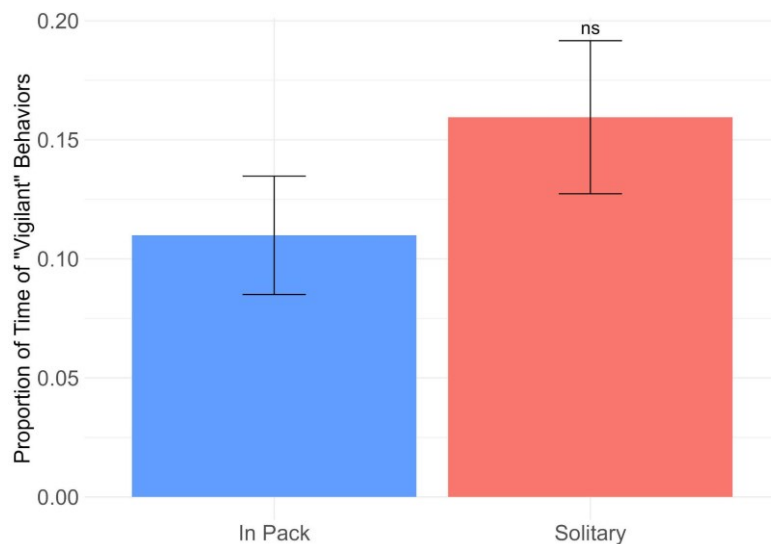
## RESULTS

**Figure 1.** Proportion of time of “Vigilant” behaviors during the test conditions.



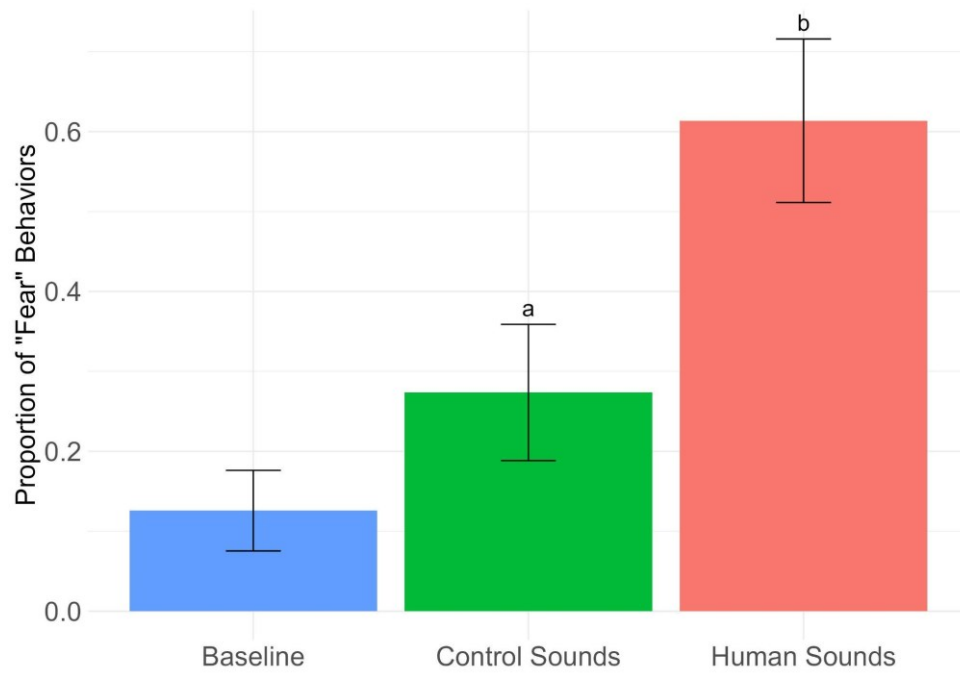
The proportion represented is calculated as the sites' mean of the total time wolves spent performing “Vigilant” behaviors on the total time they were visible in the camera. Different letters on top of the bars mean a statistical difference obtained from the results of the GLMM models (Table 2, 3). Black vertical bars represent the standard error calculated as the sample standard deviation divided by the square root of the total number of sites in each condition.

**Figure 2.** Proportion of time of “Vigilant” behaviors in Solitary and in Pack Conditions



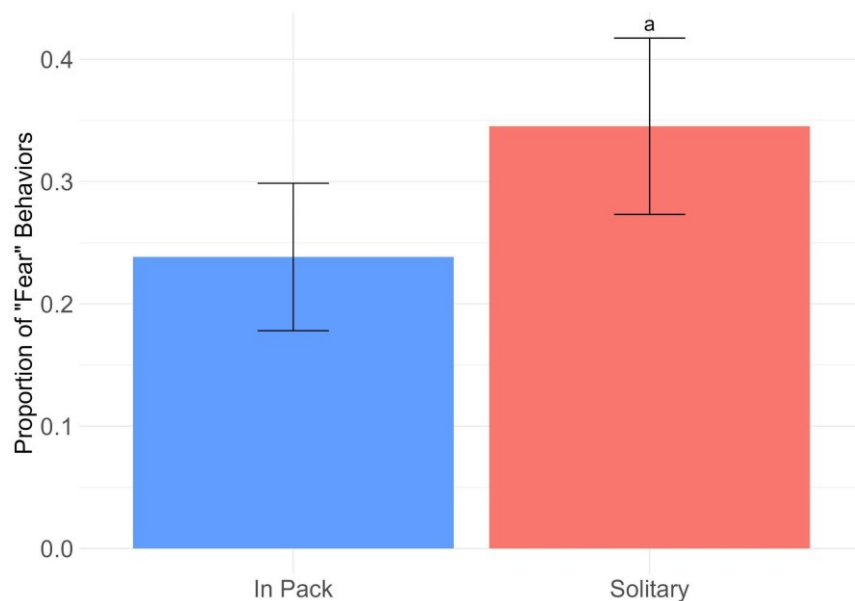
The proportion represented is calculated as the sites' mean of the total time wolves spent performing “Vigilant” behaviors on the total time they were visible in the camera. ‘*ns*’ on top of the right bar means ‘No statistical difference’ obtained from the results of the GLMM models (Table 3, 4). Black vertical bars represent the standard error calculated as the sample standard deviation divided by the square root of the total number of sites in each pack condition.

**Figure 3.** Proportion of “Fear” behaviors during the test conditions.



The proportion represented is calculated as the proportion of time wolves performed a “Fear” behavior on the total number of events ( $p$ ). Different letters on top of the bars mean a statistical difference obtained from the results of the GLMM models (Table 3, 4). Black vertical bars represent the standard error calculated as the square root of  $p(1-p)$  divided by the number of events for each condition.

**Figure 4.** Proportion of “Fear” behaviors in Solitary and in Pack Conditions



The proportion represented is calculated as the proportion of time wolves performed a “Fear” behavior on the total number of events ( $p$ ). Letter *a* on top of the right bar means a statistical difference obtained from the results of the GLMM models (Table 3, 4). Black vertical bars represent the standard error calculated as the square root of  $p(1-p)$  divided by the number of events for each pack condition.

The ‘Vigilance’ model reveals that wolves performed “Vigilant” behaviors for a longer proportion of time in the human sounds condition compared with control and baseline condition (humans vs birds: p-value= 0.0042; humans vs baseline: p-value=<1\*10<sup>-4</sup>)(Table 3, 4), and longer in the control than in the baseline condition (p-value=0.0076)(Figure 1, Table 4). No significant difference in “Vigilant” behaviors was observed between solitary and in pack conditions (p-value=0.1327) (Figure 2). None of the other control variables resulted in significant effects (Table 3).

The ‘Fearful’ model (Table 3, 4) reveals that wolves were more likely to perform “Fear” behaviors in the human sounds condition compared with the control and baseline conditions (humans vs birds: p-value= 0.0005; humans vs baseline: p-value=<1\*10<sup>-4</sup>) and higher in the control than in the baseline condition (p-value=5.8\*10<sup>-3</sup>) (Figure 3, Table 3, 4). On the other hand, the ‘Fearful’ model shows that there is a noticeable effect of the pack (p-value=0.0279), with solitary individuals showing a higher likelihood of fearful reactions (Figure 4). None of the other control variables resulted in significant effects (Table 3).

**Table 3:** GLMM model summary.

Variables	Vigilance model estimates	Vigilance model p-values	Fearful model estimates	Fearful model p-values
Control sounds	0.416	0.0027	1.637	0.002
Human sounds	0.913	2.89 * 10 <sup>-10</sup>	3.4747	4.31* 10 <sup>-7</sup>
Solitary	0.172	0.1327	0.8689	0.0279
Night	-0.067	0.648	-0.003	0.577
Human Footprint index	-0.050	0.366	-0.098	0.6661
Number event sound	-0.012	0.776	0.0356	0.7985

**Table 4:** Model estimates between conditions. Multiple comparisons are corrected by tukey method for comparing a family of 3 estimates.

Comparison	Vigilance model estimates	Vigilance model p-value	Fearful model estimates	Fearful model p-value
Control - Baseline	0.416	0.0076	1.64	0.0058
Human - Baseline	0.913	<1*10 <sup>-4</sup>	3.47	<1*10 <sup>-4</sup>
Humans- Control	0.497	0.0042	1.84	0.0005

## DISCUSSION

Across all conditions and models, wolves demonstrate a higher proportion of vigilance and fear in the presence of human sounds, compared to control and baseline conditions. This suggests that wolves could differentiate between human and control sounds, and perceive the human voice as a major threat, consistent with previous research (Crawford et al., 2022; Versluijs et al., 2022).

However, the 'Vigilance' model indicated no statistically significant differences in vigilance behaviors between solitary and group conditions, suggesting that external stimuli, rather than social context alone, drive vigilance responses. On the other hand, the 'Fearful' model showed an effect of pack presence. Our results indicate that wolves are more likely to display fearful behavior when solitary compared to when in the presence of one or more pack members, highlighting the heightened perception of vulnerability in solitary individuals. This finding aligns with the social buffering hypothesis, which suggests that the presence of conspecifics can reduce stress and fear responses by providing social support (Hennessy et al., 2009). Several mechanisms have been proposed to further explain why animals may perceive less fear when in a group. One explanation is the dilution effect, where the risk of predation or threats is distributed among multiple individuals, reducing the perceived danger for each member (Roberts, 1996). Additionally, the collective defense hypothesis suggests that groups may be better equipped to deter or confront threats, further reducing the observation of strong individual fear responses (Silk, 2007).

In the light of the social buffering hypothesis, the presence of pack members may provide a psychological sense of safety, lowering the intensity of individual fear responses when facing a perceived threat. This could explain why wolves exhibited lower levels of fearful behavior when in a group, as the social context itself may mitigate stress and anxiety responses (Moretti et al., 2015).

Recent studies have emphasized the remarkable adaptability of wolves to human-modified environments; for instance, wolves have been found living near urban settlements in densely populated areas (Zanni et al., 2023) and showing a tendency to occupy regions with high road densities where road networks are extensive (Muhly et al., 2019). These findings suggest a potential adaptation to human presence, nevertheless, in our data, urbanization did not influence the expression of these vigilant and fearful behaviors. These results indicate that, while wolves may have the ability to adapt to human-altered environments, humans still represent a significant threat to these animals. It is important to note that human presence and the human footprint do not necessarily have equivalent or parallel effects on wildlife behavioral responses (Nickel et al., 2020; Reilly et al., 2022; Suraci et al., 2021). The absence of an urbanization effect on wolves' behavior in response to human voices could

be influenced by the specific conditions of our experimental setup. In our study, the acoustic stimuli consisted of human voices, providing a direct cue of human proximity. Wolves likely interpret these auditory signals as an immediate threat, as suggested by their fearful reactions (Reilly et al., 2022; Smith et al., 2017), observed across both urbanized and non-urbanized environments.

The "event number" variable serves as a useful control for habituation because it accounts for the cumulative number of times the boombox was triggered in a given location, regardless of whether wolves were present in every instance. Even though we cannot be certain if wolves were in the immediate vicinity for every playback, repeated exposure to human voices in their environment could still contribute to a habituation process. If wolves were becoming desensitized to the stimulus, we would expect to see a gradual reduction in their fearful or vigilant behaviors over successive events. This approach ensures that our analysis considers the long-term exposure of wolves to human voices, rather than just their immediate reactions in isolated events.

Since this variable resulted not significant, the notion that human voices are particularly fear-inducing for wolves is further supported by the absence of signs of habituation to the stimuli. Similarly, the time of day did not show a statistically significant effect on wolves' responses to human voices. Wolves are nocturnal predators, used to moving and hunting during night hours (Ciucci et al., 1997), thus they might perceive less fear during nighttime. Nevertheless, our results suggest that independent of the time of day, wolves consistently perceive human voices as a threat.

Unexpectedly, the use of control sounds (tawny owl and nightingale calls) triggered significantly higher levels of fear and vigilance compared to the baseline. This is likely since these sounds were produced by electronic devices (speakers), thus introducing an unnatural element that differs from the sounds made by actual birds. This underscores the need for continued research into the technological aspects of playback studies, with the goal of reducing these potential issues and improving the reliability of the results.

These results further reinforce the concept of humans as 'super-predators' (Darimont et al., 2015; Crawford et al., 2022) and its consequences on predator behavior (Smith et al., 2015; Smith et al., 2017; Versluijs et al., 2022). Wolves in Europe have faced centuries of persecution by humans (Boitani, 2003), which has likely shaped their behavioral responses over multiple generations. Persistent hunting, culling, and eradication efforts have created strong selective pressures, favoring individuals that exhibit heightened wariness or avoidance of humans (Darimont et al., 2009). Fear responses can be learned through social transmission within packs, as younger wolves observe and adopt the cautious behaviors of older, more experienced individuals (Boitani, 2003). Additionally, over evolutionary timescales, human

persecution may have reinforced an inherited predisposition toward fearfulness, as wolves that displayed lower fear responses would have been more likely to be eliminated. Similar patterns have been observed in other species subjected to sustained human pressure. For instance, wild boars (*Sus scrofa*) in heavily hunted areas have developed increased nocturnality and a tendency to avoid open spaces, likely due to selective pressure favoring individuals that exhibit greater wariness (Cahill et al., 2012; Podgórski et al., 2018). In African elephants (*Loxodonta africana*), populations exposed to high levels of poaching demonstrate stronger avoidance behaviors toward humans and human-associated sounds, and individuals in these areas tend to be more aggressive, possibly as an adaptive response to persistent threats (Shannon et al., 2013). Similarly, many bird species in regions with intense hunting pressure have evolved greater flight initiation distances, fleeing from humans at significantly longer ranges compared to less persecuted populations (Møller & Tryjanowski, 2014). These cases illustrate how human-driven selection can shape behavioral adaptations over time, reinforcing fear responses and, in some cases, aggression in species that experience persistent anthropogenic threats. This combination of learned and possibly inherited responses ensures that fear of humans remains deeply ingrained in wolf populations today (Versluijs et al., 2022). The ongoing persecution of wolves further maintains and reinforces these fear-driven behaviors, as humans continue to be one of the leading causes of wolf mortality in Italy (Musto et al., 2021).

While the growing population of wolves is often celebrated as a conservation success, resistance to their presence persists, particularly in multi-use landscapes where livestock predation creates difficulties for both producers and resource managers (Muhly and Musiani, 2009). The conflict over wolves is a prominent example of human-wildlife conflict (HWC) and represents a crucial challenge for global conservation efforts (Musiani et al., 2009; Treves and Bruskotter, 2011).

Human-wildlife coexistence is both a social and ecological matter (Baruch-Mordo et al., 2009; Dickman, 2010; Margulies and Karanth, 2018; Manfredo et al., 2019), and wolf behavior, in particular, is deeply influenced by human actions and policies (Woodroffe et al., 2005; Drury et al., 2011; Bennett et al., 2017; Charnley et al., 2017; Frank et al., 2019; Harrison and Loring, 2020; Martin, 2021). As wolves have reestablished in multiple-use landscapes, extending their range far beyond the protected areas where ecological fear effects have typically been studied, they now encounter new socio-political environments shaped by human land use and governance systems.

A study conducted in 2019 estimated that wolves killed approximately 10,289 heads of domestic livestock in Italy, with compensation costs reaching €1,918,566 (Gervassi et al., 2019). On the other hand, a study across the EU highlights that legal killing is the most

frequently detected cause of wolf mortality in Member States where hunting or culling is permitted, however, mortality from legal hunting, culling, or traffic accidents is more frequently reported because these causes are easier to detect than poaching (Blanco & Sundseth, 2023). In Italy, however, illegal hunting remains a significant issue, accounting for 35% of wolf deaths recorded between 2005 and 2021 in the Tuscany and Emilia-Romagna regions (Musto et al., 2021). Reducing wolf-livestock conflicts necessitates addressing the human social norms, values, and assumptions about wolf behavior, which are closely intertwined with the ecological dynamics of fear (Anderson, 2022; Greggor et al., 2020). Understanding how human actions shape wolf behavior is crucial for developing effective coexistence strategies. This study contributes to the broader field of human-wildlife conflict by examining how human-induced selection pressures influence wolves' behavior. By exploring these interactions, this research aims to provide insights that can inform policy and conservation efforts to mitigate conflicts and promote sustainable coexistence.

Future research could delve into how group composition, including factors such as the number of individuals or kinship relationships, influence behavioral responses like vigilance and fear. This could provide valuable insights into the complex social dynamics underlying these reactions. Additionally, exploring how the behavior of the first individual in the group may influence the responses of others could help clarify the mechanisms of social learning and risk assessment within groups. Leader-follower dynamics have been observed across various species, where individual differences in boldness and decision-making influence collective behavior. For instance, in schooling fishlike sticklebacks, bolder individuals often take on leadership roles, impacting group movement and foraging success (Jolles et al., 2017). Similarly, in domestic horses, bold individuals are more likely to initiate movement, although their leadership effectiveness depends on social networks and affiliations rather than boldness alone (Briard et al., 2015). Moreover, stress responses can be socially transmitted within groups, influencing collective behavior. Stressed individuals may signal stressors to others, leading to changes in group dynamics and performance (Brandl et al., 2022). Investigating such dynamics in wolves could shed light on whether similar patterns exist and how they affect risk perception and decision-making. Understanding these interactions could improve appropriate management and decrease conflicts (Musiani et al., 2009; Treves and Bruskotter, 2011).



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